A NEW METHOD OF REPRODUCTION IN OBELIA

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In view of the eminence of *Obelia* as a zoological type enthroned in all text books, and the consequent widespread study of innumerable specimens, it is surprising that there could be an important method of reproduction of this genus so far unreported.

The observations recorded here were made in the course of extensive investigation of growth and form in *Obelia,* involving day by day study of specific colony sites through the summer of 1947 at Boothbay Harbor. Temperature changes were followed closely since colonies of *Obelia* and other hydroids fluctuated greatly, disappearing and reappearing as temperatures rose and fell markedly above and below 20° C. Three species were studied, all associated with one float, *Obelia articulata, O. geniculata* and *O. longissimus.*

For nearly two months of excessively high temperatures during July and August, no colonies could be found. With the onset of offshore winds, the warm surface water blew out of the bay, to be replaced by bottom water 8 to 10 degrees colder. With this lowering of the temperature, small *Obelia* colonies appeared in relatively large numbers. Calm weather with no wind except the daily inshore breeze allowed the surface bay waters to warm up again to about 21° C. for a few days, followed by a slow fall to lower temperatures. The growth or reproductive procedures described here were responses to these changes.

Obelia articulata

This species grew attached to laminaria. Colonies are relatively small but well branched, and in general are intermediate in character between the single unbranched stems of *O. geniculata* and the enormously long and branching colonies of *O. longissimus.* The intermediate character is again shown in the distribution of the gonangia. In *O. geniculata* they grow out from the angles made by the hydranths and the stem. In *O. longissimus* they appear at the angles made by hydranths with lateral branches but only at the basal region of a colony after it has already become massive. In *O. articulata* they appear when the colony is small, but at angles between hydranths and secondary branches, not in connection with the main stem. Similarly the growing tip of the main stem in colonies of all three species varies in series. It is essentially a stolonic type of growth like that of the creeping stolons. In *O. longissimus* it grows rapidly and vigorously, giving off secondary stolonic outgrowths regularly at a certain distance from the tip, and these behave in much the same way. Hydranths are mainly tertiary outgrowths, at least. In *O. geniculata* terminal stolonic growth is very limited, lateral branches are not formed, and the tip itself usually differentiates into a hydranth. *O. articulata* lies between.

In any species a rise in temperature, especially when in excess of 20° C., tends to maintain or promote stolonic growth at the end of a stem or branch of any order and conversely to inhibit hydranth differentiation. The outgrowths capable of responding in one way or another to different temperature conditions may be of varying origin. They may be the terminal tips of the main stem and secondary branches, tips of branches of a more subsidiary order, or the tips of presumptive gonangia at stem or branch angles.

A marked rise in temperature results in prolonged growth of a stolonic character in the first two cases, the long slender branches thus formed remaining an integral part of the colony, even though they may in no way contribute to its welfare. In the third case, those normally destined to become gonangia, the reaction is different.

A gonangium in its earliest recognizable stage is shown in Figure 1A, growing from the non-annulated region immediately below a hydranth. It consists of an outgrowth with several annulations, terminating in a relatively large bulb with a short central cone and wide shoulders. This persists and grows as the distal cap of the gonangium. In the same figure on the same scale are shown outgrowths from homologous locations, but from colonies subject to higher temperatures. Annulated growth, instead of stopping after two or three annulations and forming the wide gonangium rudiment, continues until ten or a dozen shallow annulations have occurred. The final surge corresponding to the establishment of the gonangium leads instead to the formation of a massive elongate stolonic structure with no further trace of annulations. It is similar to the terminal stolonic growth at the ends of branches, but with two differences, it is much more massive and of greater girth, and is so vigorous that the stem uniting it to its point of origin becomes attenuated to the point of rupture (Fig. 1B). Distally each such mass grows rapidly, while it resorbs correspondingly at the proximal end. The separation usually occurs at the region where the annulated growth transforms into a steady surge (Fig. 1C), the part left attached to the colony retracting proximally as the tension is relaxed, while the congested terminal units slide out of the thin but wide perisarcal tube to float freely in the surrounding water.

The question that arises at once is whether this is a normal process or a response to the disturbance of collection and subsequent examination. Obelia and similar hydroids are notoriously susceptible and it is a common experience to find hydranths and other terminals in process of regression with distal parts of the coenosarc often isolated within the perisarc from the main body. This possibility was considered immediately, and the following is the evidence that the process is a normal one for the sea temperature prevailing at the time. Colonies picked off the laminaria and dropped into formalin within a few seconds of emergence from the water exhibited the phenomenon to as great a degree as any. The colonies under live examination were fresh, had hydranths with active tentacles and manubrium, possessed hydranth buds that progressed normally to complete development, and showed no trace of resorption at any of the terminals.

Small colonies left standing in finger bowls liberated literally hundreds of gonangial terminals overnight and were still in active process the following day. Lastly, there is the evidence that they possess a useful function. In the first place, fragments of ordinary terminals of equivalent length but smaller diameter can reattach and survive for a week or two. They do not develop hydranths unless

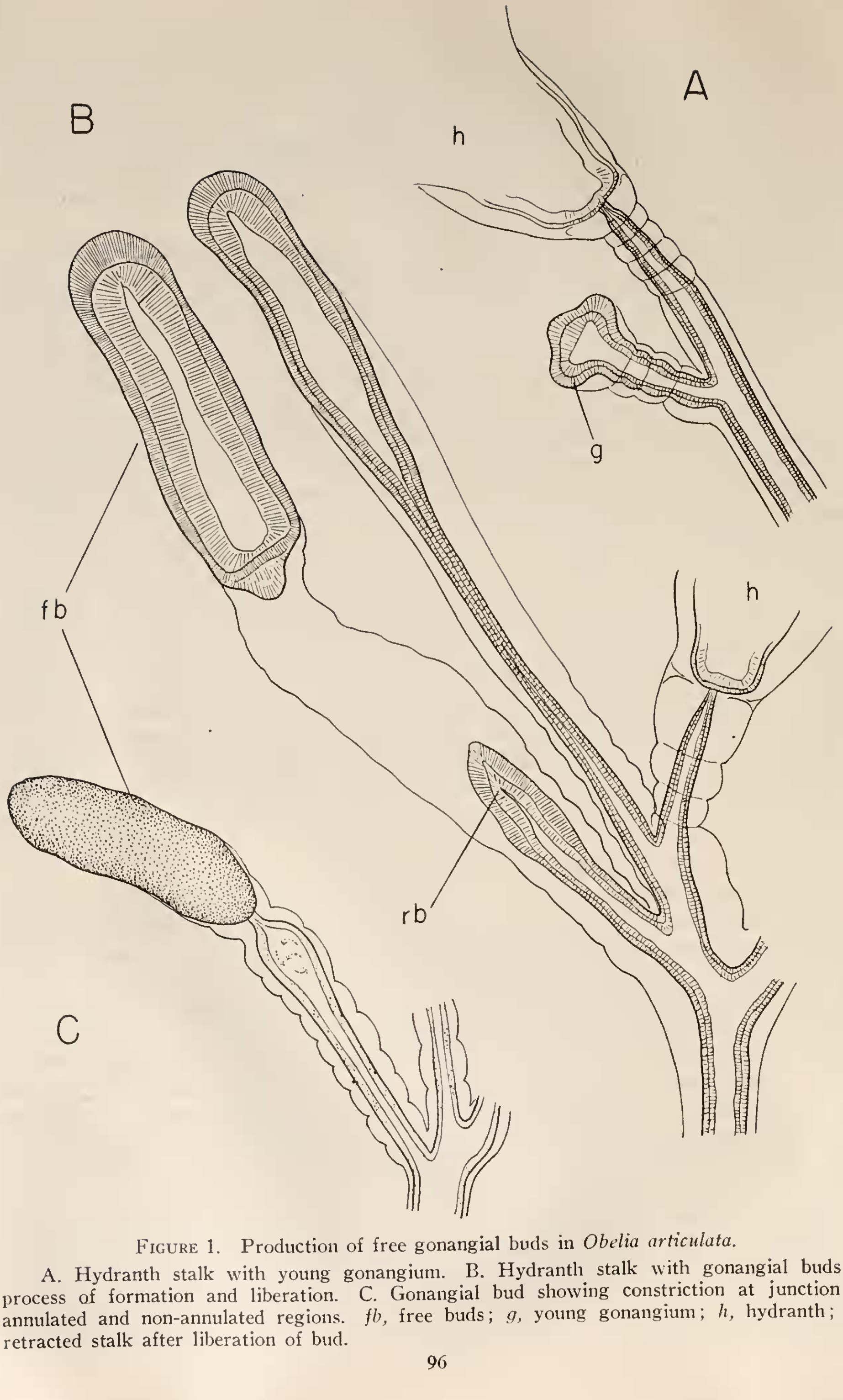

FIGURE 1. Production of free gonangial buds in *Obelia articulata.*

A. Hydranth stalk with young gonangium. B. Hydranth stalk with gonangial buds in process of formation and liberation. C. Gonangial bud showing constriction at junction of annulated and non-annulated regions. *fb,* free buds; *g,* young gonangium; *h,* hydranth; *rb,* retracted stalk after liberation of bud.

several times as long. The isolated gonangial terminals on the other hand become attached to a solid substratum immediately upon contact. After about 12 hours, each fragment is about twice its original length and half its girth. The original perisarc, however, indicates that most of the tissue is now the result of new distal growth and proximal resorption (Fig. 2B). At the same time an annulated up-

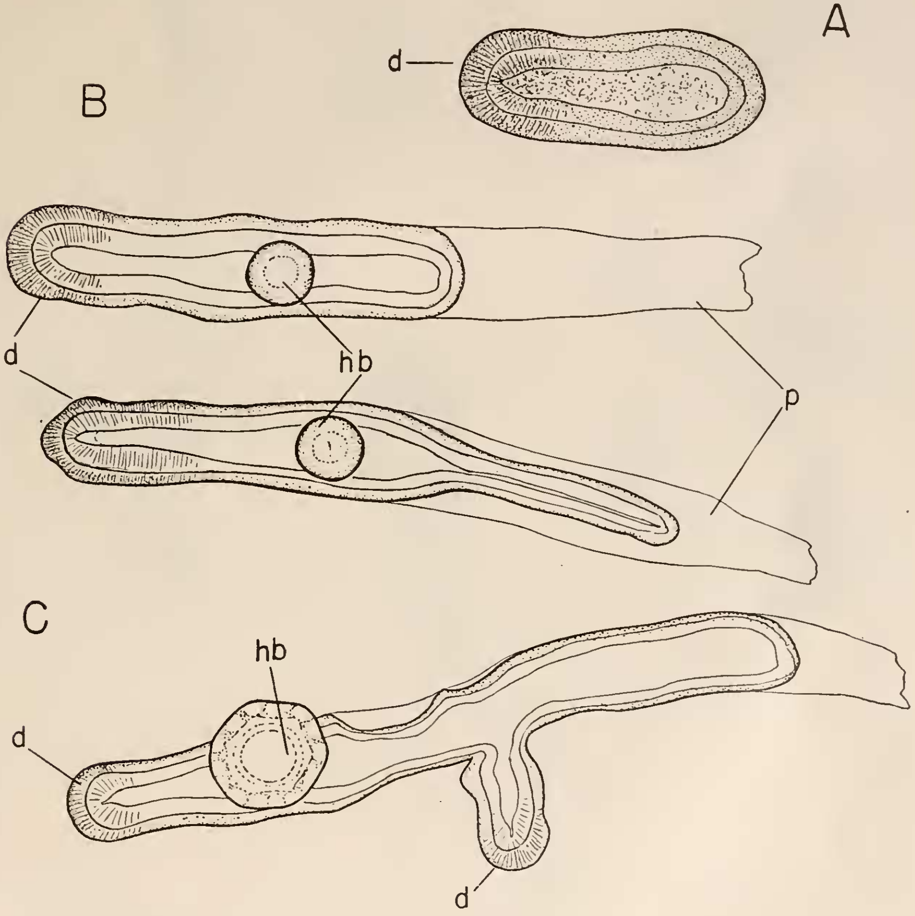

FIGURE 2. Development of free gonangial bud of *Obelia articulata*.

A. Bud at time of attachment. B. Twelve hours later with hydranth buds growing vertically and empty perisarc indicating extent of proximal resorption and distal growth. C. Twenty-four hours after attachment, with hydranth bud at tentacle rudiment stage, and with secondary distal outgrowth. *d*, distal growing region; *hb*, hydranth bud.

growth from the middle of the fragment indicates a developing hydranth. In Figure 2C a fragment is shown typical of the condition 24 hours after liberation. A lateral creeping stolonic terminal has started, while the hydranth has progressed to the tentacle rudiment stage. In the great majority of the liberated fragments, functional hydranths were present on the second day and new colonies thus started.

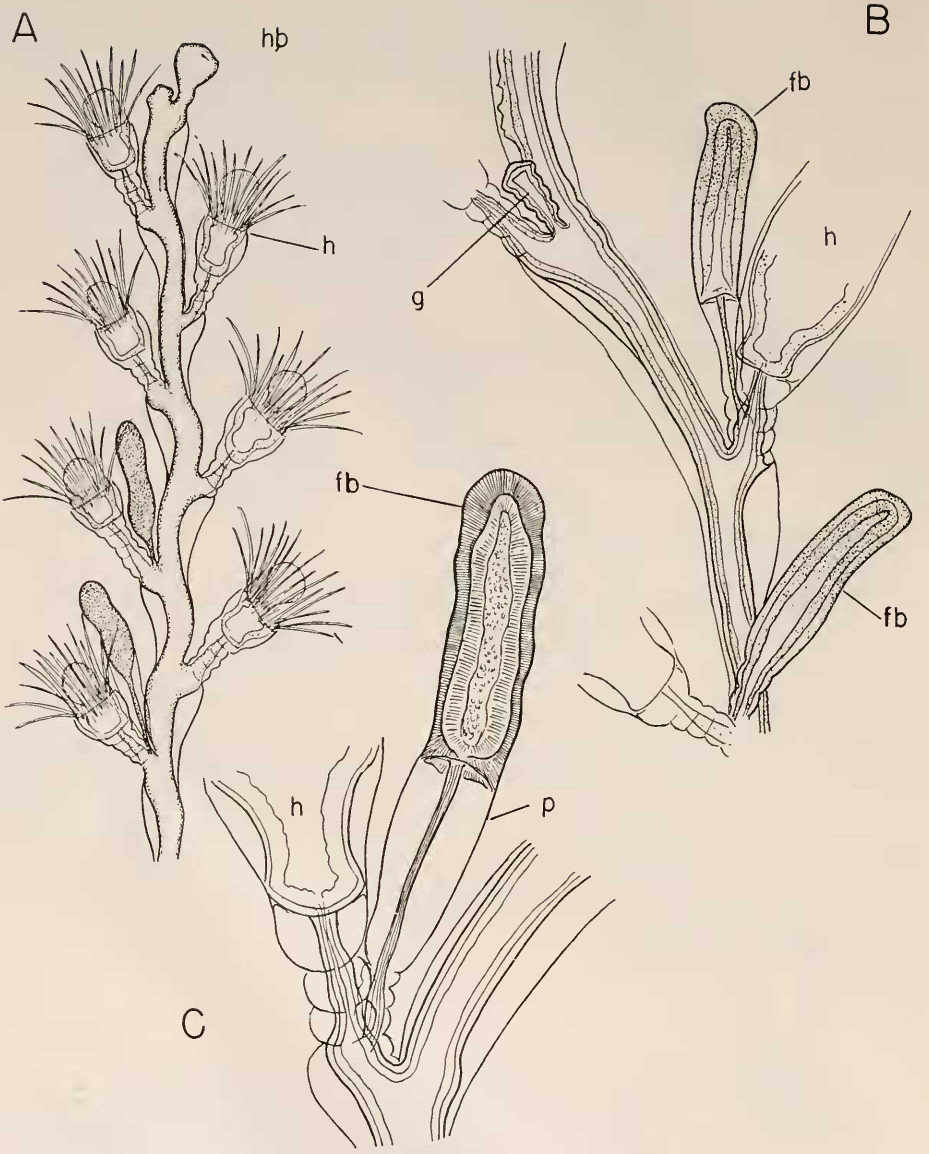

FIGURE 3. Production of gonangial buds in *Obelia geniculata*.

A. Complete sprig with two advanced gonangial buds. B. Part of stem showing young gonangium and two stages in production of gonangial buds. C. Bud showing sharp demarkation between massive presumptive free bud and attenuated proximal stalk. *fb,* presumptive free bud; *g,* gonangium; *h,* hydranth; *p,* perisarc.

The immediate developmental capacities are accordingly somewhat superior to those of the average planula.

Obelia geniculata

Colonies of *Obelia geniculata* were collected a day later than those of *O. articulata*, when the water temperature was already falling. The great majority of stems had the appearance shown in Figure 3A. No gonangia were present, but in their place were large congested terminals similar to those of *O. articulata*. Detail as seen in Figure 3C indicates that the process is essentially the same, the distal part of the massive stolonic outgrowth growing rapidly at the expense of proximal tissue. In fact the proximal half of the outgrowth becomes so attenuated that the lumen is obliterated. While actual separation was not observed in this species, continued distal growth after the occlusion of the lumen must inevitably result in a break in the attenuated proximal part. In Figure 3B two stages are shown, one with an attenuated stalk and a younger stage with wide lumen throughout. A third, the most anterior, is a younger outgrowth and is developing into a typical gonangium, suggesting that the external temperature had already dropped below the critical value at the time of its initiation. At the same time it indicates the relative scale of the two forms of growth from the hydranth-stem angles, and the comparative massiveness of the high-temperatures' outgrowth.

Obelia longissima

This species is included merely as a basis for comparison. It is typified by the very extensive growth of the primary and secondary terminals, leading to the formation of relatively enormous colonies. Gonangia appear in secondary and other angles at the base of the colony only after it has attained a fairly large size. During the warmer summer months growth is directed mainly into the vigorous terminals, and there appears to be little tendency to form gonangial outgrowths at all. They are most abundant during late winter and early spring. Consequently the type of asexual reproduction just described for *O. articulata* and *O. geniculata* is here probably of very rare occurrence, if it occurs at all, for without the initiation of gonangial outgrowths of any kind, no response in either direction is possible.

Summary

A method of asexual reproduction previously unrecorded is described for *Obelia articulata* and *Obelia geniculata*.

When water temperatures markedly exceed about 20° C. presumptive gonangial outgrowths continue growth as massive stolonic terminals that rapidly constrict off, leave the colony and settle elsewhere to establish new colonies in large numbers. In size and potentiality these reproductive units somewhat exceed those of typical campanulid planulae.